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Species diversity, abundance and brood numbers of breeding waterbirds in relation to habitat properties in an agricultural watershed

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Land-use changes and the resulting habitat degradation have been regarded as the most important known causes of waterfowl population declines. We assessed the habitat requirements of waterbirds, including waterfowl, in a hemiboreal, agricultural watershed in southern Finland. We related the birds' species diversity, abundance and brood numbers on ten lakes to environmental variables, including land use characteristics as well as topographic and local biotic features. Both species diversity and pair numbers responded to land use characteristics, such as the area of agricultural land surrounding the lakes. Our results suggest that land use may reflect habitat quality, possibly in terms of resource availability and predation risk. The pair numbers of waterbirds grew along with the availability of invertebrates, an important food resource. The abundance of gulls affected the diversity, abundance and reproductive success of waterfowl positively in our study area, probably because they provided shelter from predators.

Introduction

Wetlands are ecologically sensitive and adaptive systems that need to be sustainably used and managed (Turner *et al*. 2000). They are essential ecological features in many landscapes, and provide a number of ecosystem services (Woodward & Wui 2001, Millennium Ecosystem Assessment 2005a, 2005b, Zedler & Kercher 2005, Harrison *et al*. 2010), including habitat services for wildlife (Euliss *et al*. 2008).

In recent years, land-use changes in watersheds have increasingly affected the ecological status and conservation of wetlands worldwide, diminishing their ability to provide ecosystem services (Zedler 2003, Zedler & Kercher 2005, Harrison *et al*. 2010). The principal cause of inland wetland loss worldwide has been conversion or drainage for agricultural development (Millennium Ecosystem Assessment 2005b). The primary direct drivers of wetland degradation and loss also include infrastructure development, land conversion, water withdrawal, eutrophication, pollution, overharvesting and overexploitation (Millennium Ecosystem Assessment 2005b, Rabalais *et al*. 2009, Studds *et al*. 2012).

The destruction and degradation of wetlands affect the habitats of waterbirds (DeLuca *et al*. 2008, Ma *et al*. 2010, Ward *et al*. 2010, Studds *et al*. 2012). Waterbirds are defined as bird species that are dependent on aquatic environments, while waterfowl can be defined as species belonging to *Gaviiformes*, *Podicipediformes* and *Anseriformes* as well as the coot (*Fulica atra*) (for the definition, *see* also Elmberg *et al*. 1994). Habitat changes alter waterbird communities (DeLuca *et al*. 2008, Studds *et al*. 2012). Overall, populations of waterbirds in Eurasia and Africa declined between 1999 and 2008 (Delany *et al*. 2008), land-use changes and the resulting habitat destruction being the most important threats (Wetlands International 2010).

Bird population sizes are limited by food, nest sites, predation, weather, competition, and disease (Newton 1998). Availability of nesting and resting sites is an important feature affecting waterbird abundance (Erwin 1996). Habitat quality, in particular food resource availability, has been found to affect waterfowl diversity (Elmberg *et al*. 1994) and reproductive output (Nummi & Pöysä 1995, Gunnarsson *et al*. 2004). The habitat choice of waterfowl may also be affected by heterospecific attraction (Hildén 1964, Elmberg *et al*. 1997, Väänänen 2001).

Birds are important providers of ecosystem services (Şekercioğlu *et al*. 2004, Şekercioğlu 2006), and changes in their populations and diversity may thus hamper regional sustainability. Waterbirds are essential parts of wetland ecosystems (Moreira 1997), playing key functional roles for instance as predators, herbivores and vectors of seeds, invertebrates and nutrients (Green & Elmberg 2014). Changes in waterbird populations can profoundly affect ecosystems. For instance the introduction of arctic foxes (*Alopex lagopus*) to the Aleutian archipelago induced strong shifts in plant productivity and community structure: by preying on seabirds foxes reduce nutrient transport from ocean to land (Croll *et al*. 2005).

An important ecosystem service provided by birds is that they function as bioindicators of ecological conditions (Green & Elmberg 2014). Birds are useful biological indicators because they are conspicuous, their ecology is versatile and well-known, and census methods for them are highly developed (Koskimies & Väisänen 1991, Bibby *et al*. 2000, Burger & Gochfeld 2001, Carignan & Villard 2002, Gregory *et al*. 2005, Sutherland 2006, O'Connell *et al*. 2007). Birds can function as robust indicators of the ecological condition of their habitats, as they integrate the effects of abiotic stressors acting on species at lower trophic levels (O'Connell *et al*. 2000, DeLuca *et al*. 2004, Green & Elmberg 2014). As an early warning signal, breeding success is often a more rapid and direct indicator of environmental changes than population size (Sutherland *et al*. 2004). An early warning of environmental hazards is a prerequisite for the most cost-effective management and conservation measures (Järvinen 1983).

In this study, we assess the breeding habitat requirements of waterbirds, focusing on waterfowl, in 10 lakes in southern Finland. We relate species diversity, the number of breeding pairs, and brood numbers to environmental variables, including land use and topographic features as well as local biotic features such as food resources and predation pressure. We use two types of source data: inventory data collected for the purposes of this study, and existing topographic and environmental data from national databases.

Our specific aims were (1) to assess whether waterbird species diversity reflects habitat characteristics (e.g. food resources and shelter from predation) on a local scale, and (2) to determine the importance of local environmental factors for waterfowl habitat selection and brood numbers.

Material and methods

Study area

We studied waterbird populations at 10 lakes located in the semi-agricultural watershed of the Karjaanjoki, a river in southern Finland

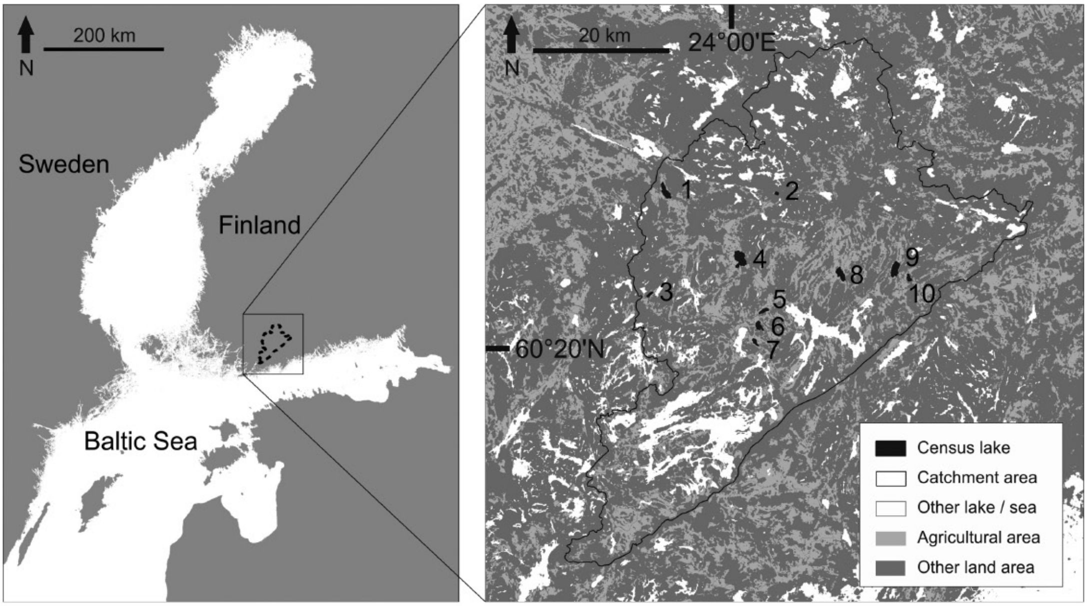

Fig. 1. Catchment area of the Karjaanjoki, a river in southern Finland, with locations of the ten study lakes. The lakes are presented in Table 1.

(60°20´N, 24°00´E) (Fig. 1). The total area of the watershed is 2046 km^2; it includes 815 lakes, of which 57 are larger than 0.5 km^2 (Teräsvuori 2003). The catchment area is located partly within the hemiboreal vegetation zone and partly within the boreal zone. The land cover structure is typical of southern Finland, i.e. a mosaic of forest (63%), agricultural areas (17.7%), and wetlands (12.2%) (Teräsvuori 2003, Kotamäki *et al*. 2009).

Natural vegetation surrounding most of the wetlands in the Karjaanjoki catchment area consists mainly of a belt of reed (*Phragmites* sp.), cattail (*Typha* sp.), sedge (*Carex* sp.), and horsetail (*Equisetum* sp.). In the case of several lakes, a high proportion of the shoreline is built up, with summer cottages, saunas and docks, or is covered by fields. The typical bird guild found on the lakes, as on most boreal breeding lakes in general (e.g. Elmberg *et al*. 2000), includes fish and invertebrate feeders: grebes (*Podicipedidae*), divers (*Gaviidae*), as well as dabbling and diving ducks (*Anatidae*).

The catchment area contains eight Special Protection Areas (SPAs) (EU 2010), including Pohjanpitäjänlahti. Five of the lakes whose area exceeds 0.5 km^2 belong to the Natura 2000 network, which along with Pohjanpitäjänlahti also covers several of the smaller lakes, as well as numerous ponds, springs, rivers and creeks (Teräsvuori & Villa 2006).

There are some 50 000 inhabitants in the area, mainly concentrated in three population centres, and to the east there is a population of about a million people (Teräsvuori 2003). Agriculture and forestry, as well as recreational activities such as fishing (Marttinen 2004), waterfowl hunting, birdwatching, swimming and other water sports (Klemola 2003) are common in the Karjaanjoki catchment area. In addition to the local inhabitants, the area is used by visitors in particular for recreational purposes (Uudenmaan ympäristökeskus 1995, Klemola 2003).

Due to the long history of human use of the watershed, it contains practically no waterbodies that might be regarded as pristine (Marttinen 2004). The main environmental pressures in the area with regard to water quality are the nutrient runoff from forestry, agriculture, industry and settlements, along with the airborne nutrient load (Uudenmaan ympäristökeskus 1995, Klemola 2003).

The Karjaanjoki catchment area has been monitored according to the requirements of the EU Water Framework Directive (EU 2000) and Habitats Directive (EU 1992), as well as in reference to national interests (Teräsvuori 2003, Marttinen 2004, Teräsvuori & Villa 2006). There have been a number of local, regional and national initiatives to enhance the condition and sustainable use of the waterbodies and the biological diversity in the area, including the Karjaajoki LIFE project in 2001–2005 (Teräsvuori & Villa 2006).

Recently, the ecological status of the majority of the surface waters in the drainage area has been classified as moderate and good (3 and 4 on a scale from 1 to 5; Finnish Environment Institute 2013). Only four of our study lakes have been classified; the status of two of them (Pusulanjärvi and Oinasjärvi) was moderate and that of the other two (Averia and Vanjärvi) poor (Finnish Environment Institute 2013).

When selecting our target lakes, we applied three criteria: the potential value of the lake as a breeding habitat, size (allowing a survey covering the whole lake), and location within the catchment area. We chose lakes representing different sizes, trophic states, settings (forest or agricultural areas), and locations within our study area, and thus representative of the entire area.

Local biotic features

Bird counts

The field study was conducted in summer 2010 and included an inventory of waterbird pair and brood numbers, focusing on waterfowl, as well as the pair numbers of night-singing birds. All other birds observed during these inventories were recorded as well.

For the breeding waterfowl census, we used the methods of waterfowl point sampling (Koskimies & Väisänen 1991). The points, 1–4 per lake depending on the area and shape of the lake (Table 1), were chosen in order to allow the observers to cover the whole water area of each lake.

Two diurnal counts were conducted in May 2010 (one 3–5 May, the other 25–26 May), between 4:00 and 13:00 in relatively calm and rainless weather with good visibility. Multiple counting rounds are recommended because of differences in the breeding phenology of species: for example the mallard (*Anas platyrhynchos*) is an early breeder, whereas the wigeon (*Anas penelope*) is a late one (Koskimies & Väisänen 1991). Following Koskimies and Väisänen (1991), some species pair numbers should be estimated in late May or early June, since birds recorded during early May (the time of our first session) may be migrants and thus not breed in the area. Nevertheless, recent climatic changes have led birds to breed earlier in the Nordic countries and in the United Kingdom (Crick *et al*. 1997, Visser *et al*. 2006, Møller *et al*. 2010, Knudsen *et al*. 2011). We may have slightly underestimated the number of some bird species (such as land birds), if the birds spotted during the first session were already nesting during the second session and were not observed.

Table 1. The lakes studied with lake code (*see* Fig. 1), name, area, number of sampling points, numbers of waterbird and waterfowl species and estimated numbers of pairs observed.

Lake code	Lake name	Area (ha)	Number of sampling points	Number of waterbird species/pairs	Number of waterfowl species/pairs
1	Oinasjärvi	106.3	4	17/33	8/19
2	Ylimmäinen	11.2	2	11/14	5/8
3	Kylänalanen	17.0	2	27/24	9/13
4	Pusulanjärvi	209.8	4	11/73	5/42
5	Koisjärvi	36.2	3	36/46	14/35
6	Musterpyynjärvi	53.9	5	14/40	8/25
7	Savijärvi	26.5	2	22/83	12/23
8	Vanjärvi	99.3	3	10/252	4/134
9	Averia	138.1	4	14/53	4/25
10	Kotojärvi	31.2	2	17/21	7/13

The census of night-singing birds was carried out during a single warm and calm night, between 21 and 22 May from 22:00 to 4:00. During the count, all singing individuals were recorded following Koskimies and Väisänen (1991).

The size of the breeding population (pair numbers) for each species at each lake was based on the number of adults or equivalents (Koskimies & Väisänen 1991). For species not specified by Koskimies and Väisänen (1991), we used the higher number of pairs recorded during the waterfowl counts and the night-singing bird census. If no individuals of a certain species were identified during the first waterfowl counting round but some were observed during the second round, the pair number was based on the second counting round also for those species for which it should be based on the first counting round according to Koskimies and Väisänen (1991). This was the case for e.g., the common snipe (*Gallinago gallinago*).

The brood numbers of waterfowl were assessed by brood counts between 29 June and 2 July. The age class of anatid chicks was estimated according to the classification by Pirkola and Högmander (1974).

For the analyses, we chose species that can be regarded as dependent on water environments and thus defined as waterbirds (Table 2). In the analyses of brood numbers, we used 14 waterfowl species belonging to *Podicipediformes* and *Anseriformes* (Table 2), as there were no broods of the other waterfowl taxa on the lakes studied. The same set of waterfowl species was used for the analyses of waterfowl species number. The maximum number of gulls was used in the analyses as an explanatory variable indicating shelter from predation (cf. for the common black-headed gull Väänänen 2000). Three gull species were present in our study area: mew gull (*Larus canus*), great black-backed gull (*Larus marinus*) and common black-headed gull (*Larus ridibundus*) (Table 2).

Food resource assessment

We assessed the availability of invertebrates and seeds in the water column (following Arzel *et al*. 2009) (Table 3), as they are the main food resources for several waterfowl species, including both adults and juveniles (Dessborn *et al*. 2011, Brochet *et al*. 2012), and good indicators of the trophic status of wetlands (Elmberg *et al*. 1993).

The sampling was conducted twice for each lake, the first time between 26 and 27 May 2010, the second between 30 June and 3 July 2010. Data from the first sampling represent the food resources available at the beginning of the breeding season, when the pairs select their habitats and prepare for breeding, and were thus used for the analysis of waterbird and waterfowl pair numbers. In the analysis of waterfowl brood numbers, we used the data from the second sampling in order to match the brood period of our target species.

We conducted the sampling along the shorelines of the lakes, where dabbling ducks were seen foraging and/or where prints (faeces, footprints, feathers) indicated recent foraging activity, in order to ensure that samples represented food items encountered by foraging ducks.

Dabbling ducks are foraging from the water surface to depths reachable by up-ending (e.g. until approximately 35 cm in the mallard) (Thomas 1982). Aquatic invertebrates were caught using 1-l activity traps (Murkin *et al*. 1983, Elmberg *et al*. 1993), placed horizontally along the shores at depths ranging from the water surface to approximately 35 cm in order to cover the feeding depths of dabbling ducks. Eight traps were used at each site on each sampling occasion.

The activity traps were in operation for 24 hours. The contents of the traps were then passed through a 0.3 mm mesh sieve, corresponding to the smaller inter-lamellae distance in the bills of ducks, which determines the minimum size of food items that ducks can catch effectively (Nudds & Bowlby 1984, Tolkamp 1993). Fish and newts were also counted, as they could affect the reliability of trap catch data by foraging on the invertebrates in the traps (Elmberg *et al*. 1992). Invertebrates were counted and identified to order or family.

Activity traps assess the abundance of epibenthic and nektonic invertebrate prey available to foraging ducks at trapping time, which is not necessarily (nor does it aim at being) a measure of the overall productivity of a wetland. Catches by activity traps cover all invertebrates, including dipterans before they emerge. Activity trap catches are thus a good indicator of food resources directly available to waterfowl, and they also reflect the food resources that will be

Table 2. Waterbird species studied. Waterfowl species used in the analyses of waterfowl species number and brood numbers are marked with '+'.

Species name	Common name	Waterfowl analyses
Acrocephalus arundinaceus	Great reed warbler	
Acrocephalus dumetorum	Blyth's reed warbler	
Acrocephalus schoenobaenus	Sedge warbler	
Actitis hypoleucos	Common sandpiper	
Anas acuta	Pintail	+
Anas clypeata	Northern shoveler	+
Anas crecca	Teal	+
Anas penelope	Wigeon	+
Anas platyrhynchos	Mallard	+
Anas querquedula	Garganey	+
Anthus pratensis	Meadow pipit	
Ardea cinerea	Grey heron	
Aythya ferina	Pochard	+
Aythya fuligula	Tufted duck	+
Botaurus stellaris	Bittern	
Branta canadensis	Canada goose	+
Bucephala clangula	Goldeneye	+
Calidris temminckii	Temminck's stint	
Charadrius dubius	Little ringed plover	
Crex crex	Corncrake	
Cygnus cygnus	Whooper swan	+
Egretta alba	Great egret	
Emberiza schoeniclus	Reed bunting	
Fulica atra	Coot	
Gallinago gallinago	Common snipe	
Gavia arctica	Arctic loon	
Gavia stellata	Red-throated loon	
Grus grus	Crane	
Larus canus	Common gull/mew gull	
Larus marinus	Great black-backed gull	
Larus ridibundus	Black-headed gull	
Mergus albellus	Smew	
Mergus merganser	Goosander	
Numenius arquata	Curlew	
Numenius phaeopus	Whimbrel	
Philomachus pugnax	Ruff	
Pluvialis apricaria	Golden plover	
Pluvialis squatarola	Grey plover	
Podiceps auritus	Horned grebe	+
Podiceps cristatus	Great crested grebe	+
Podiceps grisegena	Red-necked grebe	+
Rallus aquaticus	Water Rail	
Sterna hirundo	Common tern	
Tringa erythropus	Spotted Redshank	
Tringa glareola	Wood Sandpiper	
Tringa nebularia	Greenshank	
Tringa ochropus	Green Sandpiper	
Tringa totanus	Redshank	
Vanellus vanellus	Lapwing	

available to passerines after the invertebrates have emerged (Nummi *et al*. 2013).

Seed samples were collected with a cylindrical corer (12 cm tall, 8.5 cm in diameter). Five samples of the same volume (681 cm^3) were collected in the vicinity of the activity traps at each lake. The upper level of the sample core was at the water surface. The cores thus assessed the abundance of seeds available to foraging ducks.

Each core was emptied into a plastic bag for later sorting and identification of the contents in the laboratory, where the contents were passed through several sieves. The smallest sieve had a 0.3 mm mesh size as with the invertebrate samples (*see* Arzel *et al*. 2009). All seeds were then sorted and identified under a binocular microscope.

The sampling methods were standardised among sites. The catch from each trap and seed sample corer was analysed separately. In the analyses, we used the mean number of food items per trap.

Landscape features

Spatial data from national databases used in this study are terrain topography (as contours and points) (National Land Survey), watershed limits (Finnish Environment Institute), agricultural parcels (Statistics Finland), surface water properties (Finnish Environment Institute), and CORINE Land Cover (European Environment Agency).

We used the ArcGIS software (ESRI 2011) to calculate a set of environmental parameters for each lake to reflect the differences in their surroundings (Table 3). The basic geometrical parameters include lake surface area and perimeter, distance from the closest other lake, and percentage of the water surface of other lakes within a distance of 1 km.

We built a raster elevation model of the study area, using the most detailed vector elevation data available, the Finnish Terrain Database (National Land Survey of Finland). With this model, we computed lake-wise parameters characterising the distribution of different elevation classes (break values of 2 m above lake level) within 200 m from the lake. We also computed the average slope angle within 20 m of the lake shore.

In addition, we used the CORINE Land Cover classification to characterise the lakes based on land use patterns in their surroundings. We computed the percentage of the CORINE classes 'artificial surface', 'agricultural land', 'forest', 'wetland' and 'water' within 20 m and 200 m of the shore.

Table 3. Habitat characteristics used as explanatory variables. 'Trap' refers to the activity traps of aquatic invertebrates. 'CORINE' variables refer to the CORINE classification. Buffer zones were calculated from the lake shoreline.

Variables	Description
Local biotic	
Seeds	Mean number of seeds per sample
Invertebrates<03	Mean number of invertebrates of the size category of < 0.3 mm per trap
Invertebrates03–25	Mean number of invertebrates of the size category of 0.3-25 mm per trap
Invertebrates25–80	Mean number of invertebrates of the size category of 25-80 mm per trap
Invertebrates>80	Mean number of invertebrates of the size category of > 80 mm per trap
Maxgull	Maximum number of gull individuals observed per count
Maxraptor	Maximum number of raptor individuals observed per count
Landscape	
Area	Lake area (m^2)
DISTC	Distance to the closest water body (m)
B20arti	CORINE artificial area (%) in a 20 m buffer
B20agri	CORINE agricultural area (%) in a 20 m buffer
B20fore	CORINE forested area (%) in a 20 m buffer
B20wate	CORINE water area (%) in a 20 m buffer
DEM02	Percentage of elevations 0–2 m above lake level in a 200 m buffer

The 20-m zone around the lakes was chosen so as to represent the feeding areas of ducks closest to the shore. For fields, a field edge of at least 0.6 m around water bodies is required in Finland. In addition, there may be a buffer strip of 3–10 m or a buffer zone of at least 15 m between fields and water bodies, but with regard to waterbird habitats these wider buffer strips, covered by cultivated vegetation, can be regarded as parts of fields.

Statistical analyses

All statistical analyses were performed with R ver. 3.0.2 (R Development Core Team 2011).

We initialised the statistical analyses by reducing the number of predictors. Given our small sample size, the inclusion of all predictor variables at once would have produced numerically unstable estimates.

The number of predictors was first reduced by assessing the correlations between the variables and secondly by considering their importance, using the statistical package *MuMIn* ver. 1.9.13 (http://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf). We omitted collinear variables from the analyses (Graham 2003), as the parameter estimation becomes unstable if there is multicollinearity between parameters. Among the correlating variables, we chose those that were biologically most meaningful.

Parameters omitted from the analyses included landscape characteristics calculated from the CORINE data for a 200 m buffer zone around the lakes, the percentage of wetland area in a 20 m buffer zone, the percentage of water area in a 1 km buffer zone, the average slope angle in a 20 m buffer zone, and lake perimeter.

We finally ended up with a set of 14 explanatory variables, of which 7 were local biotic habitat characteristics based on the field study and 7 were landscape features based on the map databases (Table 3). The maximum number of gull individuals was not used as an explanatory variable in the analysis of the pair number of waterbirds, as the variable covered the pair numbers of gull species.

The four dependent variables used were the total number of waterbird and waterfowl species per lake and the total pair number and brood number of the 14 waterfowl species per lake.

We analysed the data using the *lm* function in the *lme4* package, and an information-theoretic model selection approach for statistical inference (Burnham & Anderson 2002), provided by the package *MuMIn*. We first fitted local biotic and landscape variables separately, as we expected both variable sets to affect our dependent variables. We then combined the statistically most important parameters revealed by the separate analyses of local biotic and landscape parameters, to assess their relative importance and to choose the models that best fitted our data.

We used the second-order Akaike's information criterion AIC_c that is corrected for small sample sizes to evaluate the relative support for the different models (Burnham & Anderson 2002). We considered models for which the AIC_c values differed less than four units from the model with the minimum AIC_c value ($\Delta AIC_c < 4$).

For each model, the distribution of the variables included was checked for normality.

Results

Habitat characteristics and bird species diversity

The total number of waterbird species recorded during the field study period in the 10 lakes studied was 49 (Table 2), with 10 to 36 per lake (Table 1). The numbers of waterfowl species per lake varied between 4 and 14 which was the maximum (Table 1).

The number of waterbird species increased with the maximum individual number of gulls and seed abundance. It also tended to increase with the area of agricultural land within a 20-m zone of the shoreline, but the effect was not statistically significant (Table 4). According to the model combining the best selected parameters, the species number of waterbirds increased with the maximum individual number of gulls and lake area (Table 4).

The waterfowl species number increased with the maximum individual number of gulls, and decreased with the area of water within a 20 m zone of the shoreline (Table 4).

Habitat characteristics and bird abundance

The pair number of waterbirds increased with the area of agricultural land within a 20-m zone from the shore, and decreased with the area of forest within the 20-m zone (Table 4). In addition, the pair number of waterbirds was significantly higher at lakes with a large amount of invertebrates of size class 3–25 mm (Table 4).

The pair number of waterfowl increased with the maximum individual number of gulls and with the area of agricultural land within the 20-m buffer zone (Table 4). According to the model combining the best selected parameters, the pair number of waterfowl increased with the maximum individual number of gulls and the area of forest within the 20-m buffer zone (Table 4).

Habitat characteristics and waterfowl brood numbers

The waterfowl brood number was significantly greater in lakes with the largest maximum number of gulls (Table 4). In the case of landscape variables, we did not find any statistically significant effects, but in the best model the brood number seemed to decrease with the area of forest within the 20-m buffer zone (Table 4).

Discussion

Effects of local biotic features

The increase of waterbird and waterfowl species diversity and the pair number of waterfowl with the abundance of gulls is probably due to heterospecific attraction, as some duck species are commonly nesting at lakes used by aggressive colonial breeders such as larids (Hildén 1964, Väänänen 2001). Larids may provide shelter from predators to ducks in defending their own nests (Hildén 1964, Väänänen 2001), and their alarm calls are exploited by other species for early warning to avoid predation (Pöysä 1989, Väänänen 2001, Dessborn *et al*. 2012). A gull colony can thus be regarded as a 'protective umbrella' for breeding ducks (Väänänen 2001).

Table 4. Relationships between local biotic/landscape habitat characteristics and pair/species numbers of waterbirds and waterfowl and brood number of waterfowl in the best models chosen according to AIC_c values. Analyses were run separately for landscape and local biotic variables and their combinations. Models are presented with effect estimates of habitat variables. AIC_c = Akaike's information criterion adjusted for small sample size.

Dependent variable		Best model	*F* (df1,2)	*p*	*r*	AIC_c
Species number of waterbirds	Local biotic	Maxgull (0.131 ± 0.018) + Seeds (0.038 ± 0.011)	35.87 (2,7)	< 0.001	0.91	61.40
	Landscape	B20agri (0.288 ± 0.140)	4.238 (1,8)	0.074	0.35	75.35
	Combined	Maxgull (0.130 ± 0.016) + Area (5e-06 ± 1e-06)	49.58 (2,7)	< 0.001	0.93	58.41
Species number of waterfowl	Local biotic/Combined	Maxgull (0.048 ± 0.010)	21.52 (1,8)	0.002	0.73	43.84
	Landscape	B20wate (−0.574 ± 0.215)	7.154 (1,8)	0.028	0.47	52.22
Pair number of waterbirds	Local biotic	Invertebrates03-25 (11.766 ± 3.365)	12.23 (1,8)	0.008	0.6	112.93
	Landscape/Combined	B20agri (2.713 ± 0.746) + B20fore (−1.358 ± 0.550)	12.93 (2,7)	0.004	0.79	112.74
Pair number of waterfowl	Local biotic	Maxgull (0.660 ± 0.122)	29.48 (1,8)	< 0.001	0.79	94.91
	Landscape	B20agri (1.861 ± 0.396)	18.4 (1,8)	0.003	0.70	98.41
	Combined	Maxgull (0.987 ± 0.122) + B20fore (0.964 ± 0.275)	41.82 (2,7)	< 0.001	0.92	90.74
Brood number of waterfowl	Local biotic/Combined	Maxgull (0.023 ± 0.009)	5.95 (1,8)	0.041	0.43	43.84
	Landscape	B20fore (−0.049 ± 0.022)	4.897 (1,8)	0.058	0.38	44.62

The increase in the waterfowl brood number with the abundance of gulls may be explained by the better survival of duck broods in the presence of gulls. The presence of a gull colony can considerably reduce the predation rate of waterfowl nests, as observed for example for the pochard (*Aythya ferina*) and tufted duck (*Aythya fuligula*) (Väänänen 2000, 2001).

Large gull species such as the great black-backed gull and the herring gull (*Larus argentatus*) are also important predators of ducklings (Hario & Selin 1989), but in this case the benefits gained by protection from predation apparently outweigh the costs of the pressure from gull predation. Our data, however, may not reveal the full effect of predation by gulls on the numbers of broods and fledged individuals, as we did not follow the broods throughout the brood rearing period. The mortality of ducklings is largely concentrated in their first weeks (Hildén 1964, Hario & Selin 1991, Paasivaara & Pöysä 2007), and ducklings in age classes II–III (small half-grown–almost fully-grown) have passed the most critical phases in terms of predation (Hario & Selin 1989, Mikola *et al*. 1994, Paasivaara & Pöysä 2004). In our data, of the broods for which the age class was defined, 17.6% were in age class I and thus still vulnerable to predation by gulls.

According to our results, both species numbers and pair numbers of waterbirds increased with the abundance of food in the water column. Waterbird species number increased with the abundance of seeds probably because seeds are an important food resource for many waterbird species. The abundance of seeds may reflect the lushness of vegetation in the lakes. Elmberg *et al*. (1993) found that structural diversity of the habitat affects the species number of dabbling ducks, with the highest number of species breeding in lakes with the most luxuriant and diverse shore vegetation. The fact that the waterbird pair numbers increased with the abundance of invertebrates probably reflects the importance of invertebrate food resources for waterbirds at breeding time (in ducks e.g. Krapu & Reinecke 1992, Dessborn *et al*. 2011).

Food abundance can be assumed to affect brood numbers through both habitat selection of breeding pairs, and duckling survival. Gunnarsson *et al*. (2004) found that food limits the survival of mallard ducklings, while Pöysä *et al*. (2000) showed that nesting mallards anticipate brood-stage food limitation in selecting their breeding lakes. Habitat selection may affect fitness considerably in e.g. teal (*Anas crecca*) nesting in boreal lakes (Elmberg *et al*. 2005). We did not find any effect of food abundance on brood numbers of waterfowl, but food abundance affected the habitat selection of breeding pairs. Our results suggest that the shelter from predation provided by gulls is a more crucial habitat feature than food resources at the brood stage of our target species.

Landscape features

The waterbird and waterfowl pair numbers increased with the area of agricultural land surrounding the lakes, and there was a similar but statistically non-significant effect on the waterbird species number. This pattern may be related to the resources available for birds in agricultural areas, the openness of agricultural habitats, and possibly a smaller predation risk than in forested landscapes (Huhta *et al*. 1996, Gunnarsson & Elmberg 2008). In addition, there are probably fewer summer cottages in agricultural areas in contrast to forested areas, and therefore there may be less disturbance by recreational activities. Human disturbance can affect waterbirds for instance by forcing incubating birds off nests, separating adults from free-ranging young, increasing nest predation, preventing access to feeding areas, and increasing energy costs if birds are forced to move when resting (Kirby *et al*. 2004). Disturbance in good habitats may also drive waterbirds to choose less profitable ones (Arzel *et al*. 2006).

Furthermore, a lake in an agricultural setting can be more eutrophic than one in a forested area, thus providing more abundant food resources. Nutrient enrichment alters the invertebrate and plant communities on which top-consumers such as birds rely (Zedler & Kercher 2005, May & Spears 2012). The effects of eutrophication are, however, not solely positive for waterbirds (Rönkä *et al*. 2005, Studds *et al*. 2012), as local abundances of fish and invertebrates can decline with eutrophication (Kennish 2002, Tománková *et al*. 2014).

The negative effect of forest cover on the waterbird pair numbers may relate to greater mammalian predation pressure (Elmberg & Gunnarsson 2007) or to a lack of open breeding habitats in forested areas. In Finnish archipelago surroundings, the tree and bush cover of islands favours crows (*Corvus corone*) and American minks (*Mustela vison*), which are important nest predators (Lemmetyinen 1971). In particular larids and their associates avoid islets with trees (von Numers 1995, Heinänen *et al*. 2008). Also in agricultural landscapes in Finland predators have been found to prefer coniferous forest habitats as living or hunting areas (Huhta *et al*. 1996). However, in agricultural areas there may be high densities of corvids, causing large nest losses (Andrén 1992).

The statistically non-significant tendency of forest cover to reduce brood numbers of waterfowl may also result from the decline in pair numbers of waterbirds with increasing forest cover around the lakes. We found, however, a positive effect of forest cover on the pair numbers of waterfowl. This may be due to the nest site needs of in particular the goldeneye (*Bucephala clangula*), which nests in tree cavities and nest boxes. Nest box availability may limit the abundance of goldeneye (Pöysä & Pöysä 2002) and goosander (*Mergus merganser*).

The decrease in the waterfowl species number with the increasing proportion of water area in the near proximity of the lakes may be due to detectability issues. As small ponds in the vicinity of lakes are often rich in food resources, birds breeding on the larger lakes may move there to feed and may thus be undetectable at the larger lakes. However, as an index of habitat connectivity, water availability around the lake might be expected to affect habitat choice. Hilli-Lukkarinen *et al*. (2011) found fewer waterfowl species settling at lakes where the surrounding bogs had diminished. The availability and usability of habitat corridors decreases the mortality rates of goldeneye broods that leave their hatching lakes (Pöysä & Paasivaara 2006). Connectivity also affects community resilience, i.e. the ability to recover from disturbance (Thrush *et al*. 2008).

That the largest among our study lakes hosted the most waterbird species is in accordance with the species–area relationship proposed in island biogeography (MacArthur & Wilson 1967). Paracuellos and Telleria (2004) stressed the importance of pond size to waterbird species richness. Elmberg *et al*. (1994) found that lake area explained most of the variation in species number in species dependent on the lake for brood-rearing.

The differences in habitat characteristics relating to the species number of waterbirds and waterfowl, respectively, are probably due to different habitat requirements of waterfowl in comparison with those of waterbirds in general or to differences in the relative importance of habitat characteristics for the subgroup of waterfowl. Potential detectability issues related to water availability near the lakes are probably more important with regard to waterfowl than to waterbirds in general. In contrast, the fact that lake size affected the diversity of waterbirds but not of waterfowl may be due to the greater ecological heterogeneity of waterbirds than of waterfowl.

Other factors affecting waterbird abundance and breeding success

Other factors that may affect the habitat selection and breeding success of waterbirds in our study area are competition and predation by fish (e.g. in similar region: Elmberg *et al*. 2010, Dessborn *et al*. 2012, Nummi *et al*. 2012). Predation pressure from avian and mammalian predators may also affect brood numbers (Väänänen 2000, Nordström *et al*. 2002) and habitat selection by adults (Gunnarsson & Elmberg 2008).

The waterfowl pair numbers may also be affected by heterospecific attraction between duck species. For instance, teals may use mallard presence as a cue of habitat quality in terms of food resources or predation risk (Elmberg *et al*. 1997). Density dependence may affect both pair numbers and breeding success of waterfowl for example through food abundance (Pöysä *et al*. 2000), nest site availability (Pöysä & Pöysä 2002), predation (Gunnarsson & Elmberg 2008), and/or pathogens (Newton 1998).

For a more comprehensive analysis of the habitat quality of waterbirds, we would need more specific land-cover data and a larger sample size of target lakes. In our land cover classes, minor features may be blurred, as for instance forests with small cabins may be classified as forests, thus masking the possible effects of e.g. human disturbance.

Management implications and future prospects

It has been argued that waterbirds respond to broad-scale changes in habitat quality and food resources but less so to local conditions (Wilson & Bayley 2012). According to our results, local habitat characteristics do affect the diversity and abundance of waterbirds and waterfowl and may affect the waterfowl brood numbers.

In addition to the physical characteristics of the breeding lakes and their surroundings, our results highlight in particular the importance of the heterospecific attraction to gulls. In accordance with earlier studies such as Väänänen (2001), our results imply that habitat requirements of colonial larids should be taken into account in the management and conservation of waterbirds and waterfowl.

When the habitat requirements of the species are known, it may be possible to use their population parameters as indicators of their habitat quality in environmental management and conservation aiming at regional sustainability. Until now, decision-makers and managers have paid little attention to the potential of waterbirds to provide early warning signals of environmental changes within a local context (Green & Elmberg 2014). Our results indicate that waterfowl and waterbird diversity and abundance can be used to assess habitat quality in terms of local resources, land use features, and biological interactions.

Our study shows that at least some aspects of waterbird and waterfowl habitats can be assessed using existing digital map data, without extensive field work, as stated by Rönkä *et al*. (2008). This type of approach is spatially explicit and uniform, as well as cost-effective. While it does not provide a comprehensive assessment of habitats, it can help in planning monitoring or management measures or in guiding further studies. Generalised habitat maps can also be utilised to extrapolate local or sample-based bird observations (Rönkä *et al*. 2008).

In addition to habitat characteristics, it is important to consider other processes affecting the populations, such as density dependence (Gunnarsson *et al*. 2013). Pöysä and Pöysä (2002) showed for the goldeneye that even though the provision of nest-boxes increased breeding numbers, density-dependence during the nesting and brood-rearing periods largely cancelled out the benefits in terms of the numbers of fledged birds. If such factors are not taken into account, management actions may not lead to the desired results.

Finally, when considering the abundance and habitat preferences of birds, as well as their habitat quality, temporal and spatial scales have to be taken into account. Wide-scale and long-term phenomena may be reflected in current local ecosystems both in terms of bird abundance and the habitat factors affecting it. The detection of changes in populations and habitat quality and the analysis of the reasons behind the changes require long-term monitoring data (Rönkä *et al*. 2005).

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